Eelgrass (*Zostera marina* L.) research in San Francisco Bay, California from 1920 to the present

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Introduction

The purpose of this review and synthesis is to place the state of knowledge regarding eelgrass beds in San Francisco Bay in the context of current management practices. In reviewing the history and findings of Bay area studies, we attempted to distill the findings into a synthesis that advances our understanding of factors influencing the Bay area eelgrass population, and utilizes findings from other highly pertinent studies outside the Bay area. We conclude with a list of non-prioritized, critical questions that we feel now deserve focus in the form of directed research. This review and synthesis is artificially constrained; because of the low diversity of seagrasses in general, findings from thousands of papers could be referenced and give insight as to what may or may not be occurring in San Francisco Bay eelgrass beds. However, because of the limited resources available, we could not justify a more comprehensive effort. This abundance of external information, taken together with the paucity of information regarding Bay area eelgrass, forced us to rely more on our intuition and personal experiences arising from our studies on the ecology and restoration of seagrasses worldwide over the last quarter-century than we would have liked. Nonetheless, we hope that our biases are constructive and not terribly misleading.

Three seagrass genera are found in San Francisco Bay – *Zostera*, *Phyllospadix* and *Ruppia* (Mason 1957; Kitting and Wyllie-Echeverria 1990; Kitting 1998). While plants in the genera *Phyllospadix* and *Ruppia*, remain relatively unstudied (Kitting and Wyllie-Echeverria 1990), eelgrass, *Zostera marina* L., one of eleven species in the genus *Zostera* (Kuo and den Hartog 2001) has been the subject of sporadic examinations since 1923. Early inquiries were designed to clarify debate relative to the taxonomic identity of *Z. marina* growing in Pacific waters and elucidate the response of individual plants to changes in seasonal temperature (Setchell 1927; 1929). To our knowledge, there were no studies of eelgrass for another half-century (Table 1). More recent investigations have

Table 1. The titles of reviewed articles demonstrate the shift in studies focused on eelgrass ecology in San Francisco Bay.

DATE	TITLES OF REVIEWED ARTICLES
1927	*Zostera marina* latifolia: ecad or ecotype?
1929	Morphological and Phenological notes on *Zostera marina* L.
1990	Seagrasses of San Francisco Bay: Status, Management and Conservation Needs.
1991	Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay
1995	Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: Role of light availability on metabolism, growth and survival.

focused on developing appropriate techniques to manage and monitor shrinking eelgrass populations within San Francisco Bay (Kitting and Wyllie-Echeverria 1990; Zimmerman et al. 1991; 1995). The recent focus on management is due, in part, to the widely acknowledged role of eelgrass as a valued habitat in Pacific Coast estuaries (Phillips 1984), the function of eelgrass as spawning habitat for Pacific herring (*Clupea harengus pallasi*) in San Francisco Bay (Spratt 1981) and the findings of a two-year study, designed to restore eelgrass adjacent to the Richmond Harbor Training Wall (Figure 1) (Fredette et al. 1987).

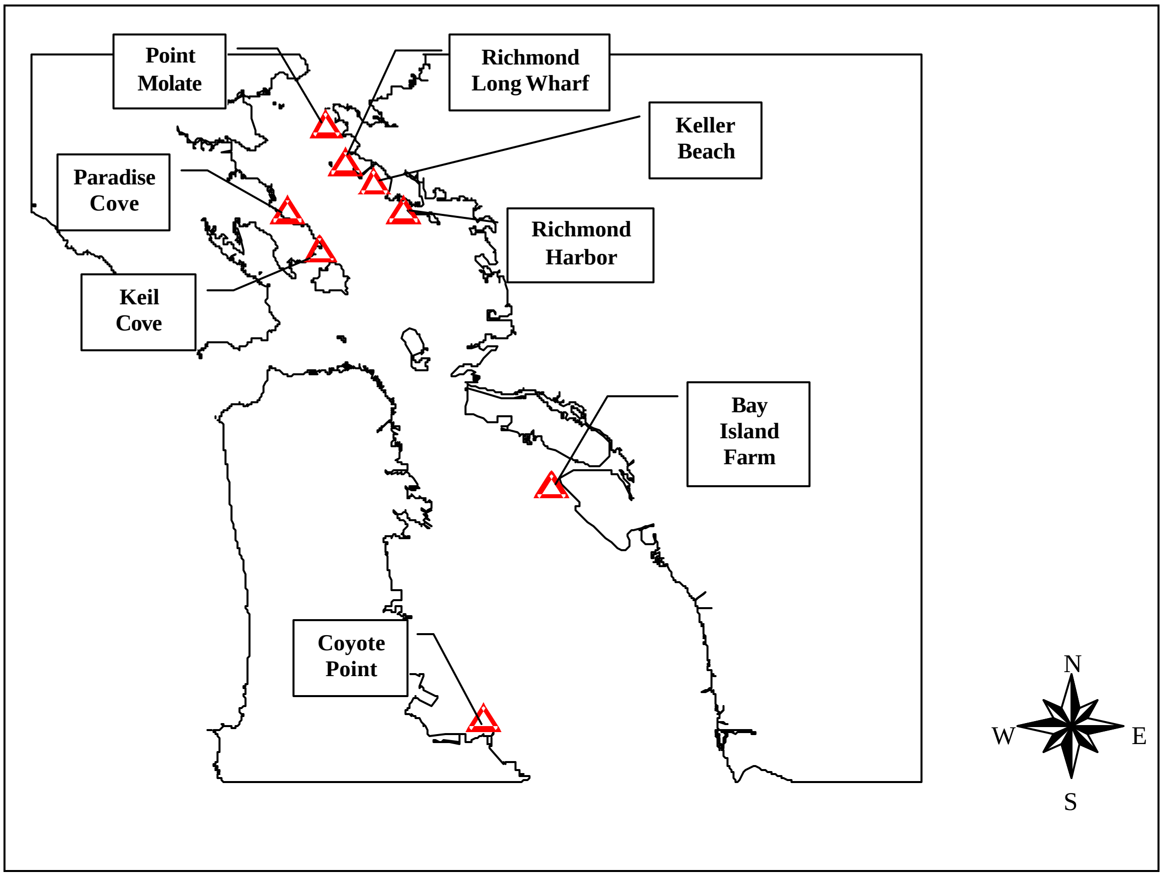

Figure 1. Historical seagrass study sites in San Francisco Bay.

Discussions surrounding the Fredette et al. (1987) publication (where the problem of annual life history strategy found for some plants in the Bay were noted with respect to traditional transplanting approaches) initiated the formation of an interagency group to evaluate the state of knowledge relative to eelgrass in San Francisco Bay (Wyllie-Echeverria and Thom 1994). The first task of this group was to execute a program to survey all areas that might support eelgrass within the Bay and estimate cover at each location.

The study, initiated in 1987, revealed that eelgrass populations were discontinuously distributed in southern San Pablo Bay, Central San Francisco Bay and the northern reach of South San Francisco Bay in 23 separate locations ranging in size from 0.5 ac (0.2 ha) to 124 ac (50 ha) with a Bay-wide estimate of 316 ac (128 ha) (Figure 1; Wyllie-Echeverria and Rutten 1989).

Secondly, because it was apparent that water column turbidity, a leading cause of seagrass decline worldwide, might be a severe problem in San Francisco Bay, an interdisciplinary effort was conducted to elucidate the relationship between submarine light and eelgrass distribution within the Bay in 1988 (Zimmerman et al. 1991). In this study, five field sites were sampled, including the two sampled by Setchell in the 1920's (Kiel Cove and Paradise Cove) and the site at the Richmond Training Wall (Figure 1). Individual leaf sections were also analyzed to clarify the light-gathering potential of eelgrass within the turbid conditions observed. Zimmerman et al. (1991) confirmed observations that water column turbidity could, in fact, limit the distribution of eelgrass both geographically and vertically within the Bay. It is particularly important to note that this study demonstrated that although San Francisco Bay eelgrass was adapted to growing in low light environments the minimum H_{sat}[1] period was between 3 and 5 hours (Zimmerman et al. 1991).

The conclusions of these two studies (Wyllie-Echeverria and Rutten 1989; Zimmerman et al. 1991), the former revealing a fragmented and potentially diminishing resource, and the latter establishing the connection between turbidity and eelgrass distribution, provided resource agencies with the necessary baseline information to recommend a management program (Kitting and Wyllie-Echeverria 1990). In response, the U.S. Army Corps of Engineers, San Francisco District required eelgrass surveys and light monitoring when navigation channels and turning basins were dredged in Richmond Harbor (Ogden 1994; CH2MHILL 1998; Merkel 1999). In addition, Zimmerman et al. (1995) designed and executed an experiment to test the potential influence of high turbidity on eelgrass transplant projects. However, the earlier issue of the two life history strategies exhibited by eelgrass in the Bay (Fredette et al. 1987), was not examined further.

While the state of knowledge has been enhanced since 1988, it is still insufficient to foster eelgrass conservation and restoration programs. There is little practical experience for eelgrass restoration in the Bay, and the poor environmental conditions of the Bay, as evidenced in what studies do exist, suggest that application of current restoration techniques will be extremely risky. In particular, the absence of information regarding annuality vs. perenniality, biological disturbance (a leading cause of transplanting failures), and spatio-temporal information on limiting factors creates the potential for highly unsuccessful transplanting by traditional methods. This is particularly troubling because it has been our experience that when early efforts fail, the enthusiasm for subsequent attempts is disproportionately dampened. Therefore, the intent of this technical memo is to: (a) review and summarize available information; (b) suggest

[1] Time of irradiance-saturated photosynthesis for each day.

additional studies and (b) recommend a prudent a course of action to guide eelgrass restoration and mitigation projects in San Francisco Bay past the early, often difficult trials of bringing this technology to a new geographic area.

The Setchell Era (1923 – 1929)

We use the term "Setchell Era" because eelgrass research during this time was guided by the sole efforts of William Albert Setchell, Professor of Botany at the University of California at Berkeley. In the 1920's Professor Setchell initiated a research program to determine the influence of water temperature on the geographic distribution of eelgrass (Setchell 1922). His findings led him to speculate on the role of temperature in the sequence of phenological expression, a theory that he tested, in part, through careful examination of eelgrass plants growing at Kiel and Paradise Coves (Figures 1 and 2).

In the midst of these investigations and, in order to resolve issues relative to nomenclature disputes regarding the taxonomic identity of eelgrass populations in Atlantic and Pacific waters, Setchell[2] (1927) compared five somatic characteristics: length of generative shoots; number of branches on generative shoots; width of leaves (vegetative); number of leaf veins and number of longitudinal ridges on the seed coat- to discriminate variety *typica* (Atlantic) from variety *latifolia* (Pacific). This work united earlier descriptions by Watson of two forms of eelgrass (e.g. *Z. oregana* and *Z. pacifica*) as *Z. marina* var. *latifolia*. Although as part of this study, field collections were made at Kiel Cove and Paradise Cove in San Francisco Bay, no other sites were sampled in the Bay (Setchell 1927). Plants from both these Bay sites were identified as *Z. marina* var. *latifolia*; voucher specimens from these sampling efforts are preserved at the University of California Herbarium and are available for examination. Each specimen carries notes of sampling date, phenological state observed (e.g. anthesis, visible fruit) and water temperature.

Based on Setchell's field observations, the relationship between temperature and phenotypic status is given in Figure 2. Field collections were frequently made through 1923-24 at Kiel and Paradise Coves (Setchell 1929). This investigation convinced Setchell that temperature was the primary controlling factor in eelgrass reproduction. In essence, he argued that as temperatures warmed in spring, vegetative growth (and seedling germination began). When temperature reached 15° C sexual reproduction was initiated. Growth slowed as water temperature increased and prolonged exposure to 30° C could result in shoot mortality. Setchell was struck by the fact that as temperatures cooled, the plants did not respond by resuming growth but rather became dormant and did not exhibit a growth response until the following spring and associated temperature increase (Setchell 1929). Phillips et al. (1983) concluded that while water temperature

[2] Setchell gave credit to his assistants Harold E. Parks and Monica Dietrich as important collaborators. Dietrich examined plant characteristics from the central Pacific coats and compared results to collections from the Atlantic coast and Parks collected developmental information and water and air temperature at Kiel Cove and Paradise Cove in San Francisco Bay.

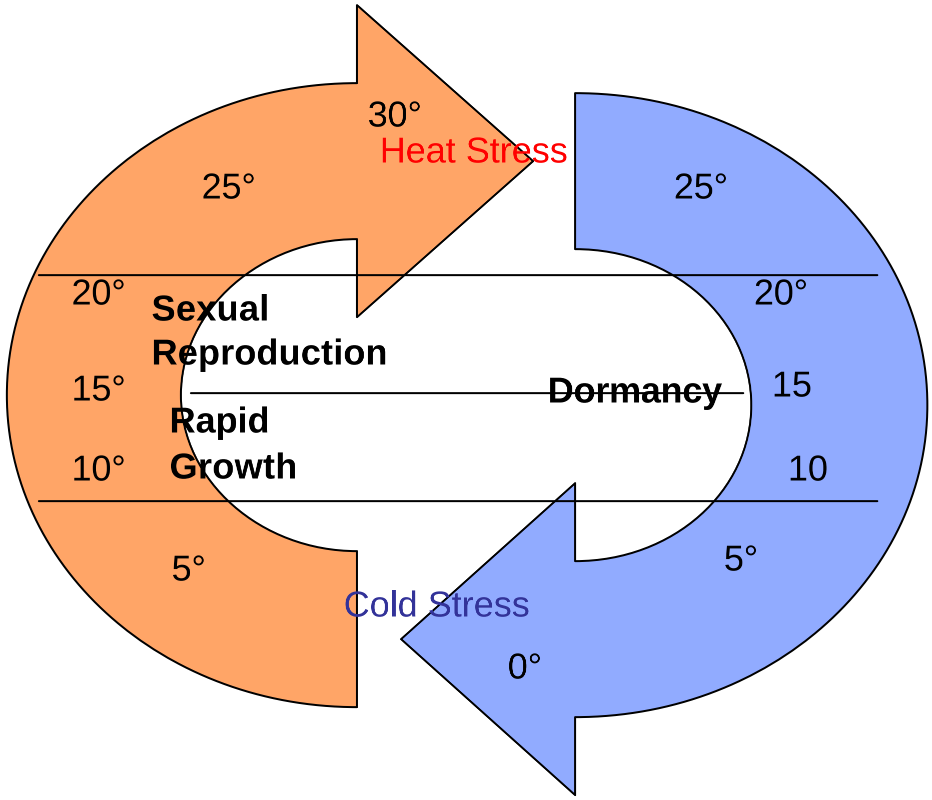

Figure 2. Graphic illustration of Setchell's topology describing the relationship between temperature and eelgrass phenology (Re-drawn from Setchell 1929).

was a factor there were other factors controlling eelgrass phenology, a position that is widely accepted but untested, although the influence of photoperiod is a likely candidate in this regard.

Two Bay studies support Setchell's earlier findings to some degree. First, as part of the Richmond Training Wall Experiment, Fredette et al. (1987) tracked the growth of transplanted seedlings in three paired plots in late April 1985. In two of the three plots seedling growth began to decrease as temperature increased in summer while seedlings in one plot recovered by late September, recovery did not occur in the other two. The experiment was terminated in May of 1986 (Fredette et al. 1987). Second are the results of a 1987 pilot study designed to test the response of seedlings to common garden conditions (Figure 3; Wyllie-Echeverria unpublished data). Seedlings were arbitrarily collected from Keller Beach (Figure 1), grown in a common garden environment (mesocosm serviced by flowing seawater) and the longest (oldest) leaf of each seedling measured. The oldest leaf of each seedling increased steadily in length during the spring but diminished fairly abruptly with the onset of warmer summer temperatures (e.g. < 20? C). When the experiment was terminated in mid July, the longest leaf of seven of the nine seedlings had either senesced or ceased to grow (Figure 3).

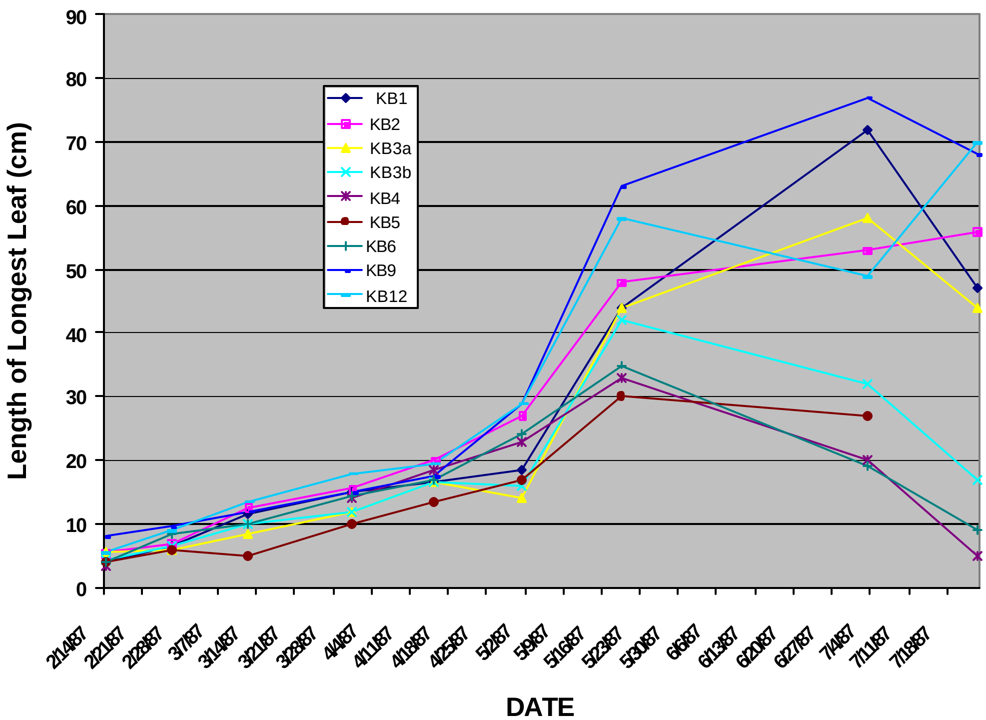

Figure 3. Seedling growth as measured by the length of the longest leaf (cm). Seedlings were grown in a common garden mesocosm.

It was clear that, as Setchell theorized and later verified by Phillips et al. (1983), temperature increase was likely a contributing factor in the biotic responses of eelgrass. This is not surprising as new growth, anthesis, seed set etc., in angiosperms is strongly correlated with temperature (Jensen and Salisbury 1984). What is more at issue is how programs designed to restore eelgrass should utilize temperature as a predictor of restoration success and performance.

Finally, while Setchell did not record information describing the distribution or density of eelgrass in San Francisco Bay, he did state that "… *Zostera marina* L. grows in extensive patches…" (Setchell 1922: Page 3). The distribution of eelgrass at Kiel Cove and Paradise cove is quite sparse by comparison to nearby estuaries such as Tomales Bay and Bodega Bay (pers. obs.). Nonetheless, this site has apparently had persistent eelgrass cover since the early part of the Twentieth Century and probably well before that time. It should receive special consideration for management and protection as a sentinel site against further water quality deterioration (and potentially, a sample of genetic structure of the population prior to the influence of European colonization).

Richmond Training Wall Studies (1984) and Afterward

As previously stated, to our knowledge, eelgrass was not the subject of scientific inquiry in San Francisco Bay from 1929 until the 1980's. Restoration efforts had not been attempted until the project implemented at the Richmond Training Wall (Figure 1). Preliminary planning began in the April 1984 with plant harvest and planting following in April of 1985 (Fredette et al. 1987). These studies indicated that eelgrass transplanting should be approached with caution in San Francisco Bay. This warning was put forward to resource agencies because (a) transplant success was marginal; (b) preliminary evidence suggested that annual populations of eelgrass might occur in San Francisco Bay (annual populations are known to exist in Baja California, Mexico and Yaquina Bay, Oregon on the Pacific coast [Wyllie-Echeverria and Ackerman 2003]) and (c) time-series information delineating the population ecology of eelgrass was lacking for San Francisco Bay. Nonetheless, the experiment contributed directly to important ecological considerations for extant eelgrass populations with studies conducted at the transplant donor site: the Richmond Long Wharf (aka Chevron Pier) as after plant harvest this site was monitored as a control. Shoot density at this control site was tracked along a depth gradient from shallow to deeper water. Control densities were highly variable during the course of the experiment. For example, shoot density in April 1985 was almost 10 times greater than that observed in July 1985; whereas shoot densities for September, 1985 and May1986 were 30% and 48 % of the April values (Fredette et al. 1987). When rhizome branching frequency data were examined for the sampling year, virtually no branching was detected during the April 1985 to July 1985 time period.

Conversely, after July, branching became more frequent, decreasing in winter and increasing again in the spring of 1986. Because branching frequency is an important indicator of vegetative colonization potential (every shoot in *Z. marina* is an apical that contributes to occupation of space as the shoots migrate across the seafloor, leaving an interwoven rhizome mat behind), we can assume that an event or series of events induced stress to the population sometime during the April 1986 to July 1986 sampling interval. It is also noteworthy that increased shoot density in 1986 was most evident in the deeper stations along the control transect. Given that one of the most prevalent stressors of seagrasses in general is lowered light availability through diminished water quality, this finding was somewhat counterintuitive. Submarine light levels are typically lower in the deeper stations, a common finding corroborated by Zimmerman et al. (1995) at Paradise Cove just to the east of the Richmond Long Wharf site (Figure 1). This hints at the emergence of shoots from germination of a seed bank in the deeper areas.

A significant finding of Fredette et al.'s (1987) was that flowering shoots were observed in clones of recently germinated seedlings. While the dimorphic expression of vegetative and flowering shoots is common in the genus *Zostera* (den Hartog 1970) when plants are in their second season of growth, its association with early life history stages generally signals the presence of an annual population (Phillips and Backman 1983).

Because incorporation of generative or flowering shoots can threaten the success of restoration projects that are designed to utilize the typically perennial contribution of vegetative reproduction in eelgrass, it would be prudent to determine where annual eelgrass plants exist in San Francisco Bay.

In the final analysis, the experiment at the Richmond Training Wall identified knowledge gaps and provided direction for continued ecological evaluation of the eelgrass resource. For example, it was clear that the lack of information on life history including seasonality and percent frequency of flowering, seedling ecology and vegetative growth rates, were a severe impediment for the planning of restoration projects, as it has been elsewhere (Fonseca et al. 1998). Also obvious were deficiencies in an understanding of relationship between nearshore environments and eelgrass survival within the Bay. In this regard, knowledge of the influence of the observed, but not quantified, turbid and sometimes very low salinity Bay waters on the geographic range and depth distribution of eelgrass was needed. Without such information, we cannot determine whether declines at Richmond Long Wharf between April and July 1985 were an anomaly or a typical seasonal fluctuation. Either way, identification of such periods of potential stress constitute a fundamental need in the planning (timing) of eelgrass restoration projects (Fonseca et al. 1998).

Concurrent with and immediately following the Richmond Training Wall experiment, several minor studies and student projects were carried out at San Francisco State University (SFSU) and California State University – Hayward (CSU – Hayward) (Kitting and Wyllie-Echeverria 1990). The focus of CSU-Hayward studies was characterization of fish and invertebrate species associated with San Francisco Bay eelgrass and their comparison with other northern California estuaries. These pilot studies demonstrated that, as seen so many times with seagrass beds around the world, species richness and density was greater within eelgrass patches than unvegetated areas. However, comparative sampling in the same year in estuaries less impacted by human development (Elkhorn Slough, Tomales Bay) revealed that the density of the similar taxa were as much as two orders of magnitude greater than found in San Francisco Bay (Kitting and Wyllie-Echeverria 1990).

Studies completed at SFSU during the summer and fall of 1986 were designed to compare flowering frequency, summer biomass, and vegetative growth rates between sites in Central San Francisco Bay (Wyllie-Echeverria 1986a; 1986b), studies that would help determine the frequency of annuality in the population and appropriate spacing for installation of planting units. Lack of replicate sampling over time reduced rigor of the studies. However, the trends described in these studies were similar to that found the more sustained studies (Fredette et al. 1987 and Zimmerman et al. 1991). For example, Zimmerman et al. (1991) noted that the ratio of flowering to vegetative shoots was high at the Richmond Long Wharf site when compared to both Kiel Cove and Pt. Molate, a location with a high frequency of annual forms of eelgrass. An abundance of flowering shoots was also noted during 1985 sampling at Richmond Long Wharf (Fredette et al. 1987). Moreover, although sampling was not sufficient at Richmond Long Wharf to compare biomass data, sampling at Kiel Cove and Pt Molate revealed that both above and below-ground biomass was higher at Kiel Cove than Pt. Molate, where light availability was comparatively reduced (Figure 4; Zimmerman et al. 1991), demonstrating a distinct, positive morphometric response by eelgrass to available light. Finally, results of a common garden mesocosm treatment, using the Plastochrone Interval (i.e., the time interval between the emergence of two successive leaves on one shoot; Short and Duarte 2001) as a proxy for new growth, demonstrated that individual shoots taken from Pt. Molate grew faster when compared to Kiel Cove, Paradise Cove and the Richmond Long Wharf when grown in a land-based mesocosm (October and November, 1986) with high light availability (i.e., Secchi depth was constantly within 13 cm of the bottom; Dennison and Kirkman 1996) throughout the experiment. The ability of plants taken from Pt. Molate to increase their growth rate in response to increased light strongly suggested that there was an environmental factor at this site limiting eelgrass growth, such as the locally high turbidity.

Additional work at SFSU included a study to determine if site-specific phenotypes of eelgrass existed in San Francisco Bay (Phillips and Wyllie-Echeverria 1989). Eelgrass from Kiel Cove and Pt Molate (Figure 1) was utilized in a common garden mesocosm (see above) experiment, reciprocal transplants among sites and leaf width measurements. Reciprocal (among site) transplants occurred in the February of 1988. All work was completed May 1988. Phillips and Wyllie-Echeverria (1989) concluded that Pt. Molate eelgrass was an ecotype (i.e., variant adapted to a local environment) while eelgrass growing at Kiel Cove was phenotypically plastic .

In an effort to specifically quantify the influence of turbidity on eelgrass growth in the Bay, Zimmerman et al. (1991) conducted experiments at five sites in Central San Francisco Bay (Figure 1), starting in the spring of 1988. In that study, field measurements of submarine light and laboratory studies to quantify the photosynthetic status of San Francisco Bay eelgrass, suggesting that while eelgrass was highly productive in this system, plants were also adapted for survival in low light, turbid environments. Zimmerman et al. (1991) also found that a high degree of variation was observed between sites with respect to the amount of light available for growth and reproduction (Figure 4). As it turned out, during that year the most suitable study sites for growth were Kiel Cove and Richmond Harbor (Figure 4). It is also interesting to note that the months of April and May were very turbid at Pt Molate and Richmond Long Wharf (aka. Chevron Pier) (Zimmerman et al. 1991). This was approximately the same time when reduced eelgrass growth had been detected in the vicinity by Fredette et al. (1987). Zimmerman et al. (1991) theorized that the low light observed in late spring was coincident with increased river flow associated with snow melt. They suggested that if this was a chronic condition, it represented more of a threat to eelgrass survival then persistent low light conditions, primarily because it was coincident with the renewal of vegetative growth and seedling establishment (see Figure 2.).

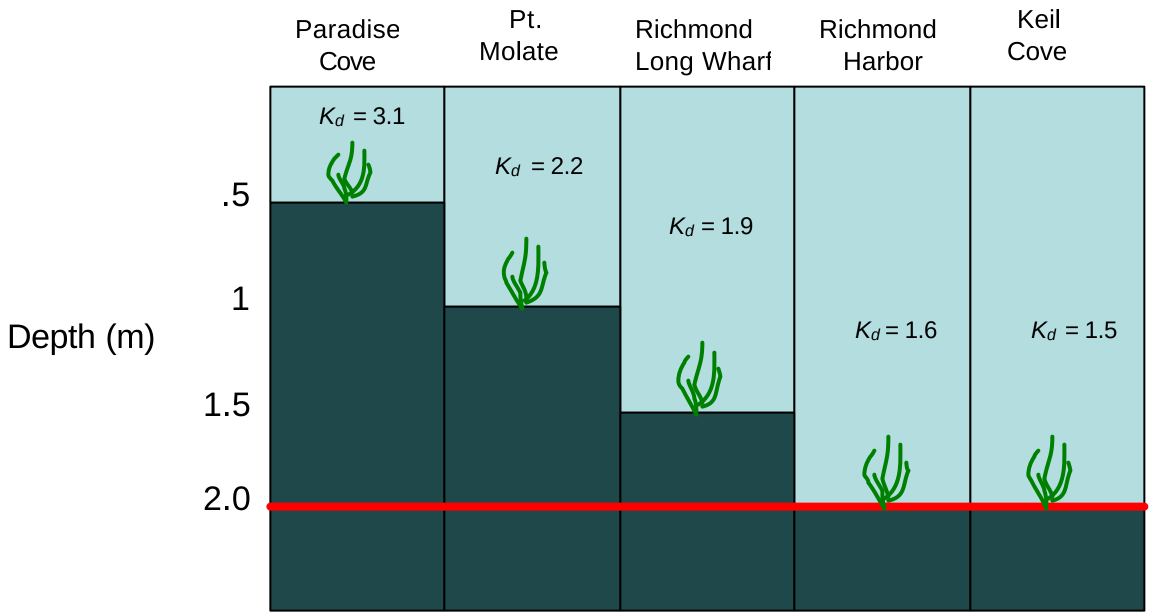

Figure 4. Variation in site specific submarine light environment influences the depth limit of eelgrass growth established during Feb – Dec. 1988 field sampling (Re-drawn from Zimmerman et al. 1991).

In response to Zimmerman et al.'s (1991) findings, the U.S. Army Corps of Engineers (ACOE), San Francisco District, required continuous submarine light monitoring to determine if dredging necessary to deepen the shipping channel in Richmond Harbor (Figure 1) would degrade water clarity over eelgrass adjacent to the channel to the degree where decreased growth or coverage would result (CH2MHILL 1998). In addition to monitoring within Richmond Harbor, the program also included data collection at Keller Beach (Figure 1), a reference site considered to be outside the influence of dredging activity. Data was recorded nearly continuously at the Keller Beach site form October 1997 to April 1998. H_{sat} was computed for each day during the sampling interval but exhibited extreme variability, however seasonal signals were evident (CH2MHILL 1998). That year, values of H_{sat} less than 8 hours occurred more frequently in winter and early spring (Table 2.). As implied by Zimmerman et al. (1991), this study also found a correlation between rainfall events and lower estimates of H_{sat} at reference and harbor sites. In fact, a common feature of heavy rainfall (>2.5 cm d^{-1}) were H_{sat} values of 0.0, an event possibly exacerbated by the presence of a storm water drain at the site (CH2MHILL 1998).

Table 2. Number of days H_{sat} was less than 8 hr d^{-1} for each sampling interval (extracted from CH2MHILL (1998)).

Sampling Period	Number of Days when H_{sat} was less than 8 hr. d^{-1}
10 Oct 1997 to 25 Nov 1997	ONE
30 Dec 1997 to 24 Mar 1998	THIRTY-TWO
8 Apr 1998 to 28 Apr 1998	THREE

Variation in turbidity within the Richmond Harbor stations, however, was such that the study determined that the dredging "caused no measurable impact to local eelgrass populations as indicated by the hours of photosynthetic saturation" (CH2MHILL 1998). Indeed, this study found that submarine light environments were more reduced at the reference site than within the harbor and, as with the Keller Beach site, a strong relationship between rainfall events and water column turbidity was found. Moreover, vessel activities, especially tugs, had a considerable, but transient, effect on water clarity. In summary, investigators recommended long-term monitoring of storm events and vessel traffic be considered in future light monitoring projects (CH2MHILL 1998).

ACOE also stipulated that prior to and following dredging, the distribution and abundance of eelgrass be determined at the site (Ogden 1994; Merkel 1999). Results of the 1994 pre-dredging survey verified that eelgrass was present along the southern side of the Richmond Harbor (Figure 1; Wyllie-Echeverria and Rutten 1989); however a new patch, just east of the harbor was also located. Polygons, delimiting eelgrass presence, were sketched on a drawing of the harbor but no estimates of acreage were included. Plant distribution within these two polygons was sparse during the August 1994 survey with densities ranging from a high of 28 shoots m^{-2} to 8 shoots m^{-2} (Ogden 1994). Fredette et al. (1987) sampled within the polygon along the southern side of the channel in the April 1985 and May 1986 and reported a range of densities between 0.6 and 19.9 shoots m^{-2}. Although at slightly different times of the year, these data are relatively indicate that while the population is sparse, it is persistent. An additional pre-dredging survey of eelgrass in the vicinity of Richmond Harbor was conducted in 1996 followed by a post-dredging survey in 1998 (Merkel 1999). While these studies verified the findings of the 1994 survey, namely that eelgrass polygons were present to the east and south of the shipping channel (Figure 1) the 1998 survey also located a very small patch to the north of the shipping channel. From these surveys, the dynamic nature of eelgrass bed extent became evident; the areal extent of the eelgrass patch on the southern side was reduced by 11.9 ac (4.8 ha) two years after dredging (but given the sampling design, declines could neither be attributed to nor divorced from dredging activity). During this same time, the reference site at Keller Beach (Figure 1) increased by 10.4 ac (4.2 ha) (Merkel 1999). Merkel (1999) suggested that there may be a link between regional weather patterns triggered by episodic events such as ENSO (*El Nino Southern Oscillation*) and the inter-annual variability observed in eelgrass populations. As a testament to the scale of coastwise variation, within a year of this observed variation in bed extent, Nelson (1997) found that both biomass and productivity increased in a subtidal eelgrass population in Puget Sound. Thus, large variation in bed extent may be expected, underscoring the need for detailed baseline (control bed) surveys concomitant with transplanting projects so as to foster reasonable expectations of restoration performance (i.e., transplant performance may be hindered during periods of natural bed contraction). Moreover, identification of causative factors when existing beds expand and contract is required to separate natural fluctuations from anthropogenic impacts, as shown by the poor controls employed in the Richmond Harbor study.

Before linkage of eelgrass bed fluctuation can be made to climatic events, it is first necessary to work out the relationship between local environmental gradients within the Bay, and the population ecology of eelgrass. The need to link environmental conditions with eelgrass restoration success was addressed when Zimmerman et al. (1995) launched an interdisciplinary study to investigate the role of submarine light in regulating the success of transplants in the Bay. As with previous work (Zimmerman et al. 1991), the 1995 work linked both laboratory and field studies. Two field sites were chosen: Kiel Cove and Paradise Cove (Figure 1), and experimental transplants, environmental monitoring and eelgrass growth studies were initiated in March of 1989 and continued until March of 1990.

Values of K_d (diffuse light attenuation coefficient of Photosynthetic Photon Flux Density) at Paradise Cove and Kiel Cove were 1.19 ? 0.32 and 0.67 ? 0.23, respectively. These values were lower than observed in 1988 (Figure 4) and sampling detected no turbidity spikes, indicating more light was consistently reaching the seafloor. The increase in available light was described as an artifact of drought conditions in the San Francisco Bay region, a condition resulting in less rainfall and river inflow. However, Paradise Cove was still a more turbid environment than Kiel Cove, which explained the complete loss of transplants in the deep water site (> -1 m MLLW) at Paradise Cove (Zimmerman et al. 1995). The shallow water transplant expanded by 20% in the first quarter of the transplant (spring to summer) but declined thereafter to 60% of original planting at the conclusion of the experiment in March 1990. This population was still present during a reconnaissance dive in 1994 (Zimmerman et al. 1995). In contrast, transplants at both shallow and deep depths survived at Kiel Cove, merging with the natural population within one year. Nonetheless, even if the total loss in the deep station at Paradise Cove is not counted, 60% of the transplants survived. The donor site, Pt Molate, was not monitored. These findings are consistent with national trends of seagrass restoration success (Fonseca et al. 1998) and further demonstrates the wide inter-annual swings in coverage that now appear typical for the Bay.

On the other hand, the survival data from Zimmerman et al. (1995) fill two critical gaps in eelgrass restoration planning. First, the fact that transplants at Kiel Cove could not be distinguished from native plants within one year of transplanting demonstrates that transplanting is a viable tool in the Bay, and second, the site at Paradise Cove was unvegetated prior to the transplant (Zimmerman et al. 1995) indicating that given appropriate environmental conditions eelgrass can be introduced in a pioneering role in the Bay. Moreover, like Kiel Cove, the Paradise Cove site may deserve special attention. Eelgrass was found at this site in 1923 and 1924 (Setchell 1929) and in 1987

(Wyllie-Echeverria and Rutten 1989; Zimmerman et al. 1991) making the location an important sentinel site for changes Bay conditions.

The utility of the environmental data became clear in this study. Although a strong seasonal signal was expressed in P vs. I parameters, there was no significant difference between sites. Thus, difference between the water quality conditions of the turbid environment in the deeper regions on Paradise Cove (that do not currently support eelgrass), and that shallow areas (where it is clear that plants will survive, grow and potentially reproduce) provides a metric for evaluation of potential eelgrass natural distribution as well as restoration in other sites with similar conditions in the Bay, although this remains to be tested.

It is also important to note that Zimmerman et al. (1995) found that carbohydrate storage in below ground organs was somewhat depleted in winter. Taken together with the very high turbidity sometimes experienced in the winter, the low temperatures and consequently slow growth of eelgrass, strongly suggests that winter plantings are not appropriate. Further evidence for this advice was nested in the finding that Zimmerman et al. (1995) verified that eelgrass survival may be at risk if events reduce the already low light available in winter and early spring, requiring plants to acclimate even more than they already must due to transplant shock when moved as planting units. A pilot transplant study conducted in 1998-99 at Bay Farm Island in Southern San Francisco Bay (Figure 1) supports this finding to some degree (Merkel 1999). Unfortunately lack of replication and randomized plot selection prevent a more general analysis, however, the data, expressed as percent survival, suggest that fall (November) and winter (February) plantings declined precipitously and did not recover during the experiment (Merkel 1999). Donor stock for fall plantings came from Bay Farm Island and Middle Harbor (adjacent to the Oakland water front; Figure 1) while winter stock was harvested from Bay Farm Island. Results of spring (June) plantings were mixed as local Bay Farm donor stock lost only 5% of the original planting by October while plants harvested at the distant site, Middle Harbor, lost 24% of the original planting in the same time interval (Merkel 1999). Therefore, a balance appears to be required in selecting planting time. For example, while spring planting may be necessary to avoid death as a result of transplant shock, winter plantings may be necessary to prevent the inclusion of annual plants in donor stock.

Summary and Recommendations

After ~20 years of sporadic studies, many crucial questions remain unanswered in order to put forward a coherent management and restoration strategy for San Francisco Bay eelgrass. Almost all these questions have to do with aspects of population ecology, as this information provides the template for what can be attempted and expected with restoration

For example, data is lacking to determine the role of seeds vs. vegetative reproduction or verify the observation that an annual population is present at particular sites. Additionally, while Zimmerman et al. (1995) provided estimates of population growth rates, these data exist for only two sites. Given the wide inter-annual variation in bed extent (a signal of a strong seed contribution to bed maintenance), and the potential for annual populations, it is difficult to extrapolate to other sites throughout the Bay.

It would also be prudent to expand sampling programs to include measurements of rhizome branching. These data were useful to interpret an observed population decline at the Richmond Long Wharf a scenario that may occur seasonally at other sites in the Bay (e.g., Richmond Harbor). These data are also crucial for determination of planting unit spacing, setting spacing guidelines for harvesting of wild stocks and the computation of recovery horizons required for and determining recovery horizons for use in Natural Resource Damage Assessment Claims Cases.

Also lacking is knowledge regarding the relative frequency of seedling recruitment, seed banks and population growth and mortality (fundamental population ecology data) in the maintenance of Bay-wide and local populations. In a detailed study Harrison (1993) documented the population characteristics of intertidal eelgrass in the Oosterschelde estuary of the Netherlands. He noted that only 13% of germinated seedlings survived and that mortality was greater at lower elevations. Given the fact that eelgrass is primarily a subtidal plant in San Francisco Bay, we suspect that seedling mortality could be greater than Harrison's recording but lack data to verify this speculation. Seedling density increased in one of the there plots monitored in the Richmond Training Wall experiment and the majority of seedlings raised in a common garden perished in the same season. The role of seed banks in bed maintenance is wholly unknown; a potentially critical factor for planning a restoration strategy (e.g., if seed banks were detected and found to be a significant source of the annual re-colonization of beds, then restoration techniques should perhaps become focused on seeding, rather than mature plant methods). Moreover, because seedlings are a small but vital component of population expansion following a disturbance and given the stress of reduced light in early spring, programs designed to scrutinize dredging activities may need adjustment during spring turbidity extremes to avoid greater than normal seedling mortality.

We do have a limited understanding of population expansion at some locations; however our knowledge is primarily driven by alien material (i.e. transplants) and studies with the existing plants were found to be rare. The obvious exception is the Richmond Long Wharf site. However even here, observations did not continue into the summer of the year following the observed decline or beyond to document the nature of the site's presumed recovery. Again, it is imperative the rate of recovery be known because it is extremely difficult to establish locally (San Francisco Bay) meaningful restoration criteria including predicted time for success and damage assessment valuations in the absence of these data.

One factor that we have not discussed is the role of biological disturbance in the ecology of natural beds, or the restoration of these beds. Throughout the world, biological disturbance has been a significant mechanism in the maintenance of bed boundaries, limitation of the colonization of new habitats, and the success of restoration efforts (see reviews in Fonseca et al. 1998). This is an unstudied aspect of Bay area eelgrass beds that should be considered as a future research goal.

To date, several studies point to water column turbidity as the primary environmental stressor controlling eelgrass distribution in the Bay. While this makes intuitive sense, it must be tested at more sites. For example, no studies have taken place in South San Francisco Bay. This relatively shallow reach of San Francisco Bay may provide opportunities for restoration (assuming historical data can be located to substantiate the presence of beds in this area), leading to the creation of eelgrass habitat within the mosaic of mudflat habitat to increase the productivity and carrying capacity of particular locations. There is a small, perhaps relic, population at Coyote Point, south of the San Francisco Airport on the west side of the Bay that was located in 1987 (Figure 1; Wyllie-Echeverria and Rutten 1989). Given the interannual variability described at more northern sites since 1987, it seems wise to survey this site again.

Additionally, the potential negative effect of storm water drainage on eelgrass populations was noted by CH2MHILL (1998) during their investigations at Richmond Harbor. To the best of our knowledge this is the first mention of the causative effect of land-based industrial, commercial and industrial operations on eelgrass health in San Francisco Bay. While this fact is widely acknowledged in other coastal states (Short and Wyllie-Echeverria 1996; Fonseca et al. 1998) it is rarely mentioned in San Francisco Bay. In fact residents seem unaware that local effects can highly modify site-specific environments. More education on this front is sorely needed and could be initiated by signage at the Keller Beach site (a City of Richmond Municipal Park) noting the findings of the CH2MHILL study.

Any meaningful discussion of water quality effects and its role in a restoration program requires establishment of a spatially and temporally useful monitoring program. To our knowledge, such data do not exist that could be extrapolated to the shallow sub- and inter-tidal areas where eelgrass occurs. While delineation of such a program is beyond the scope of this review, continually recording data loggers that register temperature and salinity, and (with a larger investment of maintenance effort), an measure of the diffuse attenuation coefficient (K_d). At the least, data collections of this sort would contribute to the creation of restoration criteria at sites not currently under consideration (vis. a vis., the Chesapeake Bay "exclusion zone" delineation; Dennison et al. 1993). Recently developed techniques (Gallegos and Kenworthy 1996) should also be employed that, through dissection of the light attenuation spectrum, can discriminate sources of turbidity that allow resource managers to identify sources and thus, set realistic strategies for creating of water column transmissivity targets.

While it is important to establish restoration criteria (e.g., Fonseca et al. 1998), it is equally important to locate restoration sites. We did not investigate the management agency permit data sets to determine where eelgrass may have been injured. However, as in the past, maintenance dredging operations are potential candidate sites, as are locations where over-water structures have been placed through eelgrass habitat. We feel that it is more important at this point is to focus on an elucidation of the population ecology of the plants and to generate a forecasting tool that would incorporate water quality criteria and the setting of water quality restoration targets, with eelgrass as the “canary” that would verify successful cleanup efforts.

Finally, it is the fiduciary responsibility of both state and federal natural resource agencies to prevent further eelgrass loss in San Francisco Bay. Toward this end, it seems prudent to fund projects that in addition to contributing to a greater understanding of eelgrass ecology also elucidate the value of eelgrass to San Francisco Bay biota. Aside from pilot studies by Kitting (Kitting and Wyllie-Echeverria 1990) and the Pacific herring census directed by the California Department of Fish and Game, only one study in the 19 years since the Richmond Training Wall Experiment was designed to articulate the value of eelgrass to Bay biota. In this study Hansen (1998) documented the vital role of eelgrass to epibenthic crustaceans. Because some of these organisms are known to support juvenile salmonids at more northern sites on the Pacific coast (Simenstad 1994), this line of inquiry may warrant further investigation. In general, we presume that as with seagrass beds worldwide, Bay area beds provide significant refuge, feeding and nursery functions for a wide variety of organisms. However, it may be much easier to generate interest in restoration efforts if the contribution of eelgrass to economically valuable species in the Bay area were reiterated.

Based on our survey of the literature, the critical outstanding questions include:

1) What is the role of seeding vs. vegetative reproduction in bed maintenance?
2) What are the major environmental stressors, when do they occur and how are these distributed across the Bay?
3) What are the appropriate seasons for planting (i.e., planting time maximizes the time since the major annual stressor that limits eelgrass growth and colonization)?
4) At what rate do vegetative plantings expand?
5) At what rate do injuries re-colonize?

6) What is the appropriate transplanting technique(s)? Should emphasis continue on whole plant transplanting or should seeding techniques be evaluated?
7) What is the role of biological disturbance, if any, in limiting restoration efforts (this has proven to be a consistent bottleneck for seagrass restoration worldwide)?
8) Where are the suitable restoration sites?
9) Can a monitoring network be established that produces a forecasting tool for setting water quality improvement targets, identification of water quality deterioration sources, and delineation of potential restoration sites?
10) What is the use of the remaining Bay area eelgrass beds by economically valuable species?

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